

THE VALUE OF IMMATURE STAGES IN EVOLUTIONARY STUDIES

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The value of immature stage characters in evolutionary studies has long been a matter of dispute (Hennig, 1966), and many workers still believe that such characters should not be taken into consideration in taxonomic research. There appear to be two reasons for this point of view. First, it is argued that, because insect larvae (especially among the Holometabola) are caenogenetic, i.e. secondary forms not resembling the ancestral condition, the characters of these early ontogenetic stages cannot be seen to recapitulate phylogeny (van Emden, 1957). Therefore, it is concluded that 'larval characters cannot be regarded as a general rule to be of overriding importance for the taxonomy' (van Emden, 1957). This view has persisted for a long time, perhaps because of the partial truth it contains. Certainly, the larvae of the Holometabola are caenogenetic; no one, as far as I know, has seriously suggested that the ancestral blowfly resembled a maggot. But this is missing the point. The point is that comparative studies of modern blowfly larvae should give us a good idea of what the ancestral maggot looked like, and thus will tell us a good deal about the evolution of the group.

The second reason put forward for ignoring immature characters is that the immature stages do not reproduce. This is a rather startling idea, since it seems to imply that immature stages are separate organisms having a gene-flow of their own, which is clearly not the case. All animals, to a greater or lesser extent, change in appearance during their ontogenetic development; in Holometabolous insects this change happens to be great and sudden, but this is hardly a reason for ignoring the pre-adult characters. In any case, immature stages do reproduce eventually and are themselves reproduced by the adult. These well-known facts seem to have caused confusion in the past. For example, van Emden (1957) states that the structure of the egg chorion reflects the shape of the follicular cells in the ovariole and that, therefore, chorionic structure is, in reality, an adult character. He distinguishes such characters from what he calls 'truly embryological egg characters'. In my opinion, this is a meaningless distinction, since both sets of characters are ultimately derived from the adult.

In principle, therefore, the characters of immature stages are equal to those of adults in value. In practice, however, it is usually found that either the adults or the larvae of a group better characterize that group. For example, Crowson (1970) states that, of the two Coleoptera families Elateridae and Carabidae, the subdivisions of the former are more clearly expressed in the larval stages, whereas the reverse is true of the latter family.

Much is often made of the fact that a classification based on larval characters will almost always be different from one based on adult characters. However, as Hennig (1966) points out, 'In many cases the asserted incongruence between larval and imaginal systems is based on the fact that only degree of similarity is considered, without raising the question of whether the similarity rests on symplesiomorphy or synapomorphy'. One may add that convergence is another question that ought to be raised. Of course, many entomologists do recognize the value of immature stages in evolutionary studies. Nevertheless, the use of these stages in such studies remains a minority activity.

Finally, it is possible that the longevity of a particular stage may be related to its taxonomic use. In the Coleoptera examples cited above, Crowson (1970) states that it may not be accidental that the larvae are long-lived and the adults short-lived in the Elateridae, whereas the reverse is true of the Carabidae. In my own limited studies on the Oestridae, which have very long-lived larvae, Crowson's point finds strong support.

The same may be true of Tachinidae, many of which overwinter as larvae (Clausen, 1940). It is well-known that the identification of tachinids is not easy, but it has hardly ever been thought worthwhile to question whether this is because the species features may be more clearly expressed in the larval stages. In a largely overlooked paper, Thompson (1922) makes the following remarks: 'It sometimes happens that species belonging to this group [i.e. Tachinidae], though easily separated by constant and well marked characters in the larval stage, are in the adult stage so similar that it is only possible to separate them by characters whose value in the group as a whole is so open to question, that to admit their validity in general would be to plunge the taxonomy of the family into inextricable disorder'. He goes on to describe three larval species parasitizing *Pyrausta nubilalis* (Lepidoptera: Pyralidae). Each of these three species consistently developed into one adult 'species', *Paraphorocera senilis* Rondani. In spite of these observations, Tachinidae specialists have continued to ignore the larvae in their definitions of species. In a group where selective pressures on the larvae would be expected to be strong, larval studies would undoubtedly be of great use in evolutionary and taxonomic studies.

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